

DIAGNOSES OF SOME NEW TAXA OF HEPATICAEE

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In several recent papers dealing with classification of the Hepaticae (Schuster, 1979, 1984) a number of new taxa of liverworts are dealt with at several distinct levels -- in most cases only in outline classifications or in synopses of groups. No opportunity existed in these cases to validate new taxa; the following Latin diagnoses are intended to provide the needed validation.

The conceptual bases for these groups are dealt with here rather briefly. They will be treated in more detail in the forthcoming treatment of the Hepaticae for Engler & Prantl, Die Natürlichen Pflanzenfamilien. In some instances only the barest minimum Latin diagnosis is given; fuller diagnoses, in English, will appear elsewhere.

1. METZGERIALES:

Pallaviciniineae Schust., subord. n. Subordo similis Blasiineis et Metzgeriineis capsulis ovoideis ad cylindricas; a Blasiineis differens ut squamae lamellatae ventrales nullae et capsula 2 valvas habet; a Metzgeriineis differens ut gametangia dorsalia et per squamas laciniaeve protecta. Type. Pallaviciniaceae.

The Pallaviciniineae appear to be sharply defined by the combination of (a) ellipsoidal to cylindrical capsules, typically opening by 2 slits, the valves coherent at the apices; (b) gametophyte often vascularized; (c) an elaterophore usually not distinct.

In addition to the type family Pallaviciniaceae, two small families appear to belong here: Sandeothallaceae (Schust.) Schust. (with only Sandeothallus) and Makinoaceae Nakai (with Makinoa Miyaki and, probably, Verdoornia Schust.).

Subfam. Podomitrioideae Schust., subf. n. Subfamilia ab aliis subfamiliis Pallaviciniacearum distincta (a) ramis gametangialibus abbreviatis, et ♂ et ♀ ramis longitudine determinatis, distincta etiam gynoeciis acrogynosis. Type. Podomitrium Mitt., an austral genus with only 2 or 3 species.

The Podomitrioideae differ from all other Pallaviciniaceae in the highly reduced latero-ventral, intercalary, gametangial branches. The ♀ branch exhibits a radial or nearly radial organization and an acrogynous condition; even if there is no fertilization, the gynoecium remains terminal. The ♂ branch is also determinate in length and the antheridia occur in 2 rows, somewhat sunken in dorsal alveoli; no discernible lamelliform scales are developed (cf. Schuster, 1984, fig. 42).

Makinoaceae subf. Verdoornioideae Schust., subf. n. Subfamilia a subf. Makinoaceis differens ut (a) antheridia dispersa, in thallo singulatim deppressa, differens etiam (b) guttae olei magnae, paucae in cellula. Type. *Verdoornia* Schust. (Schuster, 1964).

The sessile, short archegonia, with many cell rows in the highly abbreviated and hardly distinct neck are an unusual feature of Verdoornia. By contrast, in Makinoa archegonia are "normal," flask-shaped, with, typically, 5 cell rows in the elongated neck (cf. Renzaglia, 1982, figs. 325, 329-31; Schuster, 1984a, fig. 28:8). This suggests that perhaps a familial segregation between the two genera is appropriate. However, in order to avoid too many monogeneric families in the Metzgeriales, this procedure is, for the moment at least, not adopted.

The subfamily name Verdoornioideae first appears in Schuster (1966).

Subord. Blasiineae Schust., subord. n. Subordo a subordinibus propinquis Metzgeriineis et Pallaviciniineis differens ut (a) duae series squamarum ventralium planarum, etiam (b) gemmae pluricellulares praesentes, etiam (c) organa sexualia dorsalia et in cavis thalli deppressa. Type Family. Blasiaceae Klinggr.

The Blasiineae, with the single family Blasiaceae, are strikingly isolated from other Metzgeriales -- including in the ulstrastructure of the antherozoid. Both known genera are unique in the presence of specialized auriculate ventral appendages, domatia, which shield colonies of Cyanophyta.

Subord. Hymenophytineae Schust., subord. n. Subordo Metzgeriineis similis (et a omnibus subordinibus Metzgerialium insignis) ut rami gametangiales determinati reductique; a Metzgeriineis indignis ut fila ducentia thalli distincta, insignis necnon ut divisio distincta inter sistema geotropicum organorum rhizoideorum et frondes dichotomas erectas. Type Family. Hymenophytaceae Schust. (1964). Type. *Hymenophyllum* Dumort., the only genus, with 2 species.

The Hymenophytineae represent a unique end point in evolution in the Metzgeriales, the creeping, rhizoidous and "root"-bearing rhizomes plus erect, stipitate, megaphyll-like "fronds" simulating small *Hymenophyllum* spp. Although the reduced gametangial branches + vascularized thallus suggest the Podomitrioideae, the capsule and its anatomy (cf. fig. 48:1-2, 5 in Schuster, 1984) preclude any close affinity to the Pallaviciniaceae.

2. JUNGERMANNIALES:

Grolleaceae (Solari) Schust., fam. n. Familia Trichocoleaceis s. lat. atque (?)Antheliaceis cognata praecipue isophyllia; ab utraque familia insignis per (a) inopiam totam perianthii coelocaulisque, et

(b) inopiam totam ramorum terminalium ullius generis. Type. Grollea Schust.

Although sometimes placed, by others, in the Antheliaceae, Grollea is fundamentally distinct from this family in (a) lack of terminal branches; (b) lack of any trace of perianth or coelocaulus; (c) the anatomy of the capsule wall; (d) apparently 6-seriate neck of the archegonium.

Gymnomitriaceae subf. Eremonotoideae Schust., subf. n. Familia ab aliis subfamiliiis Gymnomitriacearum insignis per perianthium distinctum, emergens, plus minusve compressum, et per cellulas in foliis valde dimorphicas. Type. Eremonotus Kaal. ex Pears.

Eremonotus is a unique monotype. Its affinities to the other Gymnomitriaceae are indicated chiefly by: (a) presence of a larger-celled, unistratose, cortical layer of the axis; (b) dimorphic cells, which, much as in Prasanthus, consist of some lacking oil-bodies, while others bear 1(2) large oil-bodies.

Gymnomitriaceae subf. Stephanielloideae Schust., subf. n. Subfamilia ab aliis subfamiliiis Gymnomitriacearum insignis (a) per folia anticaliter assurgentia, echlophyllosa; et (b) per faciem anticalem axis numerosa paraphyllia chlorophyllosa habentem. Type. Stephaniella Jack.

The position of Stephaniella in Gymnomitriaceae is indicated chiefly by the fact that lateral merophytes interlock along the dorsal stem midline. In other respects the genus is totally isolated. The sporophyte, and its anatomy, need investigation.

Scapaniaceae subf. Douinioideae Schust., subf. n. Subfamilia a subf. Scapanioideis distincta (a) elateribus in una spira apparentibus, et (b) foliis cuticula ceracea obtectis, et (c) foliis obtuse complicatis, numquam carinatis. Type. Douinia (Jens.) Buch.

The Douinioideae include a single species whose position has been, and remains, controversial. It has been placed into both "Sphenolobus" (Lophozioideae) or into Diplophyllum (Scapaniaceae). The leaf form is relatively primitive; elaters are specialized. Consequently the genus does not stand in a linear relationship to any other. It is, i.a., ecologically different from Diplophyllum, none of whose species are ever epiphytic -- the normal mode of occurrence of Douinia.

Blepharidophyllaceae Schust.

Clandarium (Grolle) Schust., gen. n. [Basionym. Blepharidophyllum subg. Clandarium Grolle, J. Hattori Bot. Lab. 28:65, 1965]. Type. Clandarium clandestinum (Mont.) Schust. [Basionym. Plagiochila clandestina Mont., Ann. Sci. Nat., Bot., Ser. 2, 19:247, 1843]. Also here are C. xiphophyllum (Grolle) Schust., comb. n. [Basionym. Blepharidophyllum xiphophyllum Grolle, J. Hattori Bot. Lab. 28:65, 1965] and C. gottscheanum (Grolle) Schust., comb. n. [Basionym. B. gottscheanum Grolle, ibid. 28:69, 1965].

Clandarium is strongly distinct from Blepharidophyllum s. str. in (a) the nonspathulate, carinate leaves, much more deeply (to 0.65-0.8 bifid) lobed; cells evenly thick-walled; (b) plants reproducing by gemmae, the gemmiparous shoots erect, developing underleaves.

Balantiopsidaceae subf. Isotachidoideae Schust. subf. n. Subfamilia a subf. Balantiopsidoideis insignis (a) foliis noncomplicatis, (b) perianthia, aut eius vestigiis, ad apicem perigynii erecti, plus minusve distincti sito. Type. Isotachis Mitt.

The Isotachis complex was first recognized as a family by Schuster (1957) and later by Hatcher (1960-61), but is better treated as a mere subfamily of Balantiopsidaceae Nakai.

Mastigophoraceae Schust. The single genus Mastigophora Nees is divisible into two distinct subgenera, Mastigophora s. str. and:

Eomastigophora Schust., subg. n. Subgenus a subg. Mastigophora distinctum ut (a) folia subtransverse orientia, plus minusve symmetrice 4-lobata tamquam in Chandonanthus subg. Tetralophozia reperta, atque (b) amphigastria semper bifida tamquam in C. subg. Tetralophozia. Type. M. caledonica Steph.

Eomastigophora shows some primitive traits (mature leaves in large part subsymmetrically, deeply quadrifid) linked with one advanced feature (underleaves only about half the size of lateral leaves, always bifid). The only extant illustration of the taxon is in Schuster (1984, fig. 73:1-4).

Jubulopsidaceae (Hamlin) Schust., fam. n. Familia Lepidolaenaceis capsulis rostratis cognata, distincta, autem, ut (a) elateres spirales, (b) amphigastria plana, numquam sacca aquaria efficientia, atque (c) cellulae epidermales membranae capsulae incrassationes ad angulos nodulosos, Frullania-formes praebentes. Type. Lepidolaenaceae subf. Jubulopsidoideae Hamlin, J. Hattori Bot. Lab. 37:173. Type. Jubulopsis Schust.

Anatomy of the capsule wall is much more like that of Frullania

than of any other taxon in the Lepidolaenineae and seems to confirm the relationships drawn (Schuster, 1966, 1970) between Porellineae and Lepidolaenineae.

Radulaceae (Dum.) K. Müll.

The family includes a single genus Radula Dum., which is divisible into four subgenera, of which Metaradula Schust. (Schuster, 1980b) is new; it has not been validated; the validation follows:

Radula subg. Metaradula Schust., subg. n. Subgenus subg. Odontoradulae cognatum praesentia perigynii tubularis, pinguis, rigidi, stipitiformis, typi Isotachis sub perianthium siti; ab Odontoradula distinctum lobis foliarum rotundatis atque unico pari q̄ bractarum. Type. Radula buccinifera (Tayl.) Tayl.

In subg. Metaradula we find exactly the same kind of stalked paragynoecial "apparatus" as in Radula subg. Odontoradula: a fleshy, terete, stalklike base + a basally tubular, distally compressed, narrow perianth (cf. fig. 79 in Schuster, 1984). The fleshy base, derived from axial tissue, constitutes an Isotachis-type perigynium.

Lepidoziaceae Limpr.

This large, complex family is divided into 5-6 families (Fulford, 1968), which are inadequately based. In Schuster (1984, pp. 1023-26) 8 subfamilies are accepted, which, conceptually have nothing in common with the Fulford families. Two of the subfamilies are new:

Drucelloideae (Bosen) Schust., subf. n. [Basionym. Lepidozioideae tribe Drucelleae Bosen, Lindbergia 8:73, 1982]. Type. Drucella Hodgs. Bosen (l.c.) has added one relevant fact to the earlier detailed account in Schuster (1980a): the epidermal capsule wall cells bear nodular thickenings of all longitudinal walls, hence have a "one-phase" ontogeny. The Bosen illustration (fig. 7:4) unfortunately fails to show any trace of cell walls, hence the dimensions and form of the epidermal cells cannot be deduced. The genus, formerly assigned, albeit with a question mark, to the Lepidozioideae (Schuster, 1969, p. 11), seems distinct from this in the (a) one-phase development of epidermal cells of the capsule wall; (b) incubous leaves with insertion leaving 2 cell rows free, dorsally; (c) lack of terminal branches; (d) presence of mere oil-droplets, as distinct from oil-bodies, in leaf cells.

Neogrolleyoideae Schust., subf. n. Subfamilia Lembidioideis similis ut folia + transversa, ad apicas vadose lobulata, non profunde lobata; distincta (a) praesentia pigmentorum ferrugineorum in membrana, atque (b) trigonis nodosis, atque (c) androeciis antheridia in bracteolis habentibus. Type. Neogrolleya Hodgs.

Although placed in the Lembidioideae in Schuster (1972), because of its isolation Neogrollea was emphasized as being a "puzzling" and "relict" monotype, without clear affinities to other genera. As such, its isolation is best expressed by placing it into its own subfamily, allied to but distinct from the Lembidioideae.

Neogrollea was recollected in 1984. Living plants clearly show that there are a few, very large, botryoidal oil-bodies per cell. This feature is a significant additional criterion separating Neogrollea from all genera of the Lembidioideae.

Lejeuneaceae Cavers

The ca. 75 genera of this family remain, in many cases, inadequately investigated. Infrageneric classification of many taxa remains a puzzle. The following covers only a few of the extant problems:

Stictolejeunea (Spr.) Schiffn. Although including only some 6-7 species, the genus is very heterogeneous and is divisible into two subgenera, one with two sections, as follows:

Subg. Stictolejeunea

Sectio Stictolejeunea. Type. S. squammata.

Sectio Macrocellaria Schust., sect. n. Sectio a sect. Stictolejeunea differens ut (a) cellulæ leptodermatae, trigonis grossis, autem, praeditæ, et magnæ (cellula media ca. 18 x 18-25 μ); (b) ocelli permagni, dimorphici; duo basales ad 25 x 45 μ bini, laminis solum ca. 4-6 ocellos sparsos habentibus; ocelli defuncti fusco-brunnei. Type. S. herzogii Buchloh.

Subg. Leptostictolejeunea Schust., subg. n. Differt a subg. Stictolejeunea (a) papilla lobulorum marginalis; (b) cellulæ corticalis 12-seriatibus; (c) rami nonsexualis Lejeunea-typus. Type. S. iwatsukii Mizutani; here also S. richardsii Herz. and S. africana V. Berghen.

Differing from subg. Stictolejeunea in (a) lobular hyaline papilla inserted marginally, at base of apical tooth; (b) cortical cells in only ca. 12 rows, not in 2-3 strata, the stem only 5-6 cells high; (c) lobules of leaves ovoid, with orifice turned toward lobe apex; (d) vegetative branches all Lejeunea type.

Leptolejeunea (Spr.) Schiffn. In addition to the typical subg. Leptolejeunea, two other subgenera appear necessary for highly deviant species, as follows:

Subg. Leptosticta Schust., subg. n. Subgenus a subg. Leptolejeunea differens ut (a) ocelli per lobum dorsalem sparsi (saepe etiam 1-2 in cellulis marginalibus) saepe, autem, 2-3 in basi lobi aggregati; alii ocelli in lobula amphiastriisque sparsi; ocelli, in plantis siccatis

brunnei-rubri ad atrorubros, (b) plantae rigidae, arcte adnatae dum siccatae aut madidae, atque (c) cellulae ubique leptodermatiae sine trigonis. Type. *L. amphiophthalma* Zwickel (Ann. Bryol. 6:117, 1933); a synonym of *L. picta* Herz., Flora 35:430, 1942.

All true species of *Leptolejeunea* (e.g., subg. *Leptolejeunea*) have colorless ocelli; these are confined to dorsal lobes of leaves (and ♀ bracts). In *Leptosticta* ocelli are often dull red-brown to rust-red, much as in the unrelated *Pictolejeunea* Grolle; they occur not only in the lobes, but also in lobules and underleaves, much as in *Lepidolejeunea* Schust., to which there is also no clear affinity. Perhaps deserving of treatment as an autonomous genus.

Subg. *Asticta* Schust., subg. n. Subgenus a subg. *Leptolejeunea* differens ut (a) ocelli nulli, (b) lobi amphigastriorum biseriati in ca. 3 stratis basalibus, uniseriati solum disaliter, ca. 6 cellulis longi, atque (c) plantae siccatae virides, arcte appressi colentes. Type. *L. anopthalma* Zwickel (Ann. Bryol. 6:116, 1933).

Like subg. *Leptosticta*, subg. *Asticta* forms an anomalous element within *Leptolejeunea*. I once believed that perhaps this entity fitted better into *Rhaphidolejeunea* Herz., but the species of that genus have, at the least, one conspicuous basal ocellus, lobules with a distinct, often hooked, 1-celled apical tooth, and relatively evenly thick-walled leaf cells. In *Asticta*, however, no ocelli at all appear distinct; lobules -- as in subg. *Leptolejeunea* -- have a low, blunt apical tooth (compare, e.g., fig. 3:i in Zwickel, 1933 with Schuster, 1980, fig. 752:1); leaf cells have strong, nodulose trigones and intermediate thickenings, although toward the leaf bases these tend to be confluent. Unfortunately known only sterile; when fertile material is discovered *Asticta* may need to be elevated to generic rank.

3. MARCHANTIALES:

Marchantiaceae (Bisch.) Endl. The family was divided into two subfamilies in an outline classification in Schuster (1979, p. 78); additional study suggests that a division into three subfamilies would be better, as follows:

Subf. *Marchantioideae*: *Marchantia* Marchant f., *Preissia* Cda.

Subf. *Dumortieroideae* Schust., subf. n. Subfamilia *Marchantioideis* similis ut et ♂ et ♀ receptacula stipitata, stipibus, autem, semper satis brevibus; distincta ut (a) filamenta chlorophyllosa, si adsunt, ad vestigia ex 1(2) cellulis composita, reducta; (b) vesiculae reductae aut vestigialia aut nullae atque (c) seta sporophyti perspicue longior facta, ut in *Lunularia*. Type. *Dumortiera* Nees.

The phylogenetic position of this group remains a matter of controversy; it has been regarded, on biochemical bases, as closer to the *Conocephalaceae* subf. *Wiesnerelloideae* (*Wiesnerellaceae*), but

differs from this group in the stalked or receptacles.

Subf. Bucegioideae Schust., subf. n. Subfamilia a subf. Marchantioideis distincta ut filamenta chlorophyllosa in vesiculis nulla. Type. *Bucegia* Radian; *Neohodgsonia* Perss. probably also here.

Ricciaceae Dum. The family is commonly held to include only two genera, *Riccia* L. and *Ricciocarpus* Corda. However, recognition of a third genus seems necessary:

Pteroriccia Schust., gen. n. Genus a *Riccia* s. str. distinctum ut (a) superficies dorsalis thalli velutina ob filamenta cellulae erecta isolata atque (b) squamae ventrales ingenter, usque ad 1.5 mm long.; erectae (siccatae super thallum incurvatae), apicibus eorum serratis. Type. *Riccia villosa* Steph.; monotypic.

Pteroriccia is at least as distinct from *Riccia* as is *Ricciocarpus* -- the last universally recognized as a valid genus. The figures in Arnell (1963, p. 20), although not good, show the characteristic cross section, with the large, imbricate ventral scales erect and projecting far beyond (and far above) the thallus margins. Serrate ventral scales do not occur in *Riccia*, but do occur in the water forms of *Ricciocarpus*, to which there is, however, no close affinity.

Riccia (Mich.) L. Three subgenera are usually recognized: subg. *Ricciella*, subg. *Riccia*, and subg. *Thallocarpus*. A fourth subgenus is needed for *R. membranacea* Gottsche & Lindenb.:

Riccia subg. *Leptoriccia* Schust. Subgenus subg. *Thallocarpus* similis ut (a) thalli spongiosi, vesiculis magnis praediti, atque (b) sporae papillis disiunctioribus, potius quam reticulo obtectae. A *Thallocarpus* differens ut sporae numquam quaternae se cohaerentes. Type. *R. membranacea* Gottsche & Lindenb.

As far as known, subg. *Leptoriccia* is monotypic. I know of no species except *R. membranacea* that clearly fits here. The thalli simulate fern gametophytes -- they are thin and translucent, with very little ventral tissue developed.

4. On an anomalous new species of *Radula* Dum.

One of the "classic" genera of Hepaticae is *Nietzgeriopsis* Goebel (Lejeuneaceae) in which the vegetative gametophyte is reduced to a radiately expanded monostromatic thallus; only the sexual branches, which are very short, bear complicate-bilobed leaves, in two ranks. Closely, if superficially, similar is the following species of *Radula*:

Radula yanoella Schust., sp. n. Species subg. *Metaradulae*, sectionis Epiphyllarum ab omnibus aliis Epiphyllis differens thallo persistente, radiatim expanso, monostromatico e cuius marginibus rami determinati, breves, foliacei, atque plerumque simplices enascuntur. Type. Serra Curicuriari, Brazil (RMS 50-1691).

This unique plant consists of a closely furcate, radiately expanded, rosette-like, monostromatic thallus, growing by means of apical cells with 2 cutting faces. Eventually some or all thallus segments show a transition from such apical growth to tetrahedral apical cells and, abruptly, leafy shoots are cut off (cf. Schuster, 1984a, fig. 11 on p. 799). Aside from this, the weak axes, formed of few cell rows, clearly suggest that a species of sect. Epiphyllae is at hand. Evidently reduction in this Radula has occurred parallel with that which has occurred in Metzgeriopsis.

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